AN EARLY OCCURRENCE OF *SARCOPHILUS LANIARIUS HARRISII* (MARSUPIALIA, DASYURIDAE) FROM THE EARLY PLEISTOCENE OF NELSON BAY, VICTORIA.

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The isolated lower molar series of a dasyurid from early Pleistocene sediments at Nelson Bay, near Portland, is referred herein to *Sarcophilus laniarius harrisii* (Boitard, 1842). Dental measurements and morphological comparisons taken from this tooth series compare closely with those of the extant subspecies. The genus *Sarcophilus* is known from the early Pleistocene by the species *S. moornaensis* Crabb 1982. Fossil material assigned to *S. laniarius harrisii* is now also known from Early Pleistocene sediments. The new specimens from Nelson Bay extend the origin of *S. laniarius harrisii* to the early Pleistocene.

Key words: *Sarcophilus laniarius harrisii*, Pleistocene, Portland, Nelson Bay Formation, Dasyuromorphia, Dasyuridae.

THE FIRST reports of the occurrence of the fossil remains of the living Tasmanian *Sarcophilus* in the Quaternary deposits of Victoria were by Selwyn (1858, 1860) based on identifications by Frederick McCoy. The modern geographical distribution of the extant dasyurid subspecies *Sarcophilus laniarius harrisii* (Boitard, 1842) widely known as *S. harrisii* (Boitard 1842) is restricted to dry sclerophyll forests and coastal woodlands of Tasmania (Strahan, 1995). The fossil record of the species has a distribution on mainland Australia during the Pleistocene (Long et. al. 2002). Fossil *S. laniarius* has been recorded in many geochronologically dated Pleistocene and early Holocene terrestrial and cave fossil localities. Representative occurrences are provided in Table 1. The maximum range of the geochronologically dated specimens is no older than 0.352 +/- 1.8 Mya down to less than 10,000 years. The extinction of the species from the mainland is believed to have been the result of a failure of the species to compete successfully with the introduced Dingo *Canis familiaris dingo* (see Corbett, 1985), which occupied a comparable ecological niche (Strahan, 1995).

The earliest occurrence of *Sarcophilus* is from the early Pleistocene, with *S. moornaensis* Crabb (1982), known from a right mandible and molars, and is a member of the Fisherman's Cliff Local Fauna (Crabb, 1982). Crabb's species comes from the sands of the Moorna Formation in south western New South Wales, which is estimated to be early Pleistocene in age (Long et. al. 2002). Late Pleistocene fossil-bearing deposits in the Wellington Caves, New South Wales have yielded significantly larger specimens of *Sarcophilus*, and the species *S. laniarius* (Owen, 1838) was proposed for this material. Werderlin (1987) argued strongly that *S. laniarius* is the senior synonym for *S. harrisii*, and recognised three subspecies of *S. laniarius*, namely *S. laniarius laniarius* (Owen, 1838), *S. laniarius dixonae* (Werderlin, 1987) and *S. laniarius harrisii* (Boitard, 1842), the latter of which is also the extant subspecies. Dawson (1982) recognised the basis for diagnostic distinction of *S. laniarius laniarius* from the extant species is the larger size rather than discrete morphological differences. Murray (1991) noted that the Wellington Caves *S. laniarius laniarius* is an "essentially statistically assigned (sub) species (with) no particular morphological features other than significantly larger size and associated allometry from ...present-day Tasmanian Devils" (Murray, 1991, p. 1090-1091). As a result we accept that *S. laniarius laniarius* is a larger form of *S. laniarius harrisii*. For the purposes of this present report, we follow Werderlin's (1987) taxonomy of the three subspecies, and the binomen *S. laniarius* (Owen, 1838) has priority, as shown in Long et al. (2002).

It may be argued that the use of *S. laniarius* (Owen, 1838) as the senior synonym of *S. harrisii* (Boitard, 1841) for the living Tasmanian Devil results in the destabilization of commonly used nomenclature. While Environment Australia's biodiversity fauna list

(Environment Australia, Australian Biological Resources Study, 2002) refers to *S. harrisii* as the binomen for the living species, it is in contrast with Smithsonian Museum of Natural History taxonomic database (Smithsonian Museum of Natural History, Department of Systematic Biology, 1993) that recognizes the priority of *S. lanuarius* for the extant species. As shown by Werderlin (1987) and subsequent workers (Long *et. al.* 2002), this recognition of priority does not significantly destabilize nomenclature and is therefore retained by us.

In the late 1970's, a stratigraphical review of the sediments outcropping in Nelson Bay, near Portland, was undertaken by E. D. Gill, C. W. Mallett, J. M. Lindsay and N. W. Archbold. Archbold collected a small collection of fossil bone and tooth material from a single locality. Amongst the collected material were assorted diprotodontid, vombatid, macropodine and dasyurid mandibular and dental remains. It is the dasyurid material that is described herein and is assigned to *S. lanuarius harrisii* on the basis of dental measurements and morphology. Due to the age of the sediments that contained this material (0.73 - 1.66mya) (White, 2002), it appears that they constitute the earliest occurrence of this species.

Stratigraphy and age

Based on field notes and personal recollections from one of us (N. W. A.) relating to the locality, the unit in which the material is referred to is unquestionably the Nelson Bay Formation, located approximately 5 km south of Portland (38° 36' S., 141° 35' E.). Studies of the sedimentary processes and the formation of the bone beds which outcrop at Nelson Bay have been undertaken by Boutakoff (1963) and Kenley (1988), and were reviewed by White (2002).

The sediments of the Nelson Bay Formation were deposited in a lacustrine environment that existed at this locality at the time of deposition. The lake occupied a large subsided caldera formed from volcanic activity 2.76 million years ago (Aziz-Ur-Rhamen & McDougal, 1972). Sediments from the surrounding Portland Limestone were levelled and redeposited as sedimentary beds within the 'Nelson Bay caldera lake' (White, 2002). These sediments in turn formed calcarenite beds, interspersed with clay beds. The clay beds in the caldera lake sediments are marked by the presence of rip-up clasts formed by strong currents during periods of flooding of the lake, and form a portion of the Nelson Bay Formation.

The Nelson Bay Formation includes a distinct unconformity, forming a boundary between the Upper Nelson Bay Formation and the Lower Nelson Bay Formation. This unconformity has been correlated with the Gunz Glacial Peak (Boutakoff, 1963), implying a minimum age of 0.73my for the underlying Lower Nelson Bay Formation. The sediments of the Lower Nelson Bay Formation have been described as approximately 10m of clay beds, which includes approximately 3m of horizontally bedded calcarenite, resting on 2m of sandy clay. This in turn rests upon pink sandy clay soils (Boutakoff, 1963). It is the sandy clay soils that form the fossil bone beds in the Lower Nelson Bay Formation. The presence of the formaminiferal species *Globoratalia truncatulinoides* in the sediments of the Nelson Bay Formation implies a maximum age of 1.9my for this unit (Srinivasan & Kennet, 1981). Magnetic polarity stratigraphy studies have concluded that the Nelson Bay Formation represents an age of 1.63 – 0.71 my (Whitelaw, 1991). MacFadden (1987) noted that the Nelson Bay Formation is significant in terms of palaeontological, radio isotopic and palaeomagnetic data leading to a relatively precise geochronology for the formation (MacFadden et al 1987). Kenley assigned the Nelson Bay Formation to the Early Pleistocene (Kenley 1988, p. 366). Rich et al. (1991) also stressed that the Nelson Bay Local Fauna "is the single securely dated Early Pleistocene assemblage from either Australia or Papua New Guinea."(p. 1014). White (2002) noted that five distinct fossil bone beds are present in the Lower Nelson Bay Formation. The collection of the material described here can not be located precisely to a particular bone bed described, but it originated from the Lower Nelson Bay Formation approximately 50m west of the sewer outfall, and was at the time of collection approximately 1.5m above the beach sand in front of the cliff. The material can therefore be considered Early Pleistocene in age.

The Nelson Bay Local Fauna

Hann (1983) partially described the 'Nelson Bay Local Fauna' in an unpublished Honours thesis, which was subsequently updated by Herrmann (2000) in an unpublished Masters thesis. Whitelaw (1991) referred to the Nelson Bay Local Fauna in terms of geochronology, however the composition of this Local Fauna was not included in this reference. White (2002) compiled a list of identified fossil species from this

locality which comprise the fauna identified prior to 2000 and included additional material in the local fauna which was identified for the purposes of that study. A combined lists of species from the Nelson Bay Local Fauna is provided in Table 2.

SYSTEMATIC PALAEONTOLOGY

Subclass MARSUPIALIA Illiger, 1811

Cohort AUSTRALIDELPHIA Szalay, 1982

Order DASYUROMORPHIA Gill, 1872

Superfamily DASYUROIDEA Goldfuss, 1820

Family DASYURIDAE Goldfuss, 1820

Genus *Sarcophilus* Geoffroy Saint-Hilaire & Cuvier, 1837

Type Species *Sarcophilus laniarius* (Owen, 1838)

Selected synonymy.
Didelphis ursina Harris 1808: 176, pl. 19.
Dasyurus laniarius Owen 1838: 369, pl. 49, figs 3-7.
Sarcophilus harrisii Boitard 1842: 290, Merigian *et al.* 2002: 84, fig. 2C, fig 8A-F.
Sarcophilus (Dasyurus) ursinus Owen, 1877: 105, pl. 13, figs 2, pl. 15, fig 2.
Sarcophilus (Dasyurus) laniarius Owen, 1877: 105, pl. 5, figs 1-6, pl. 14, fig 2.
Sarcophilus satanicus Thomas, 1903: 289.
Sarcophilus laniarius laniarius Owen, 1838, - Werderlin, 1987: 9.
Sarcophilus laniarius Owen, 1838, Long *et al.* 2002: 55.

Description of material. The illustrated material collected at Nelson Bay comprises a complete lower molar series (M/1, M/2, M/3 and M/4), a single lower premolar (P/2), and canine. The material is composed of teeth only, traces of mandibular material were found associated with the suite of teeth but disintegrated on collection. There is no doubt that all the teeth derived from a solitary individual. The canine is crescentic, denuded of dental enamel and shares the robust morphology of the *S. laniarius harrisii* used for

Fig. 1. *Sarcophilus laniarius harrisii*, labial view. Scale bar intervals represent 10mm.

comparative purposes. The premolar (P/2) is composed of enamel and a single root consistent with *S. laniarius harrisii* morphology. M/1, M/2 and M/3 are complete teeth with enamel and roots intact, M/1 showing a degree of occlusal wear consistent with mature sarcophiloid dasyurids. M/4 is fragmentary (in two portions) with much of the talonid missing, break is a vertical 'crack' from protoconid. Trigonid of M4/ present, talonid is absent.

A list of 22 morphometric characteristics of the lower dentition of *S. laniarius harrisii* were recorded from 20 individuals. This morphometric data was then compared to corresponding characteristics on the Nelson Bay material, and is shown in Table 3. The Nelson Bay material is unquestionably from *S. laniarius harrisii* on the basis of this comparison.

Sarcophilus laniarius harrisii Boitard, 1842

Discussion. Considerable discussion on the dental morphology and fossil record of *S. laniarius harrisii* is available. Archer (1976) discussed dasyurid dental nomenclature and demonstrated the relationships of dasyurids (including *S. harrisii*) to didelphids, thylacinids, borhyaenids and peramelids. Archer (1982) reviewed the dasyurid fossil record (including *S. harrisii*), and investigated the phylogeny of dasyurids generally. Wroe *et al.* (2000) investigated the dental and cranial characteristics of dasyurids (including *S. [laniarius] harrisii*) using cladistic analysis for phylogenetic analysis. The dental morphological characteristics assigned to *S. laniarius harrisii* in these investigations conform closely to the Nelson Bay material. The illustrated specimen was also compared with the holotype *of S. moornaensis* and was shown to share broad morphological affinities consistent with the generic distinction of *Sarcophilus*, but was found to differ in a combination of features, such as the generally smaller size of *S. moornaensis*. The *S. moornaensis* specimens also displayed more elongate M/3 and M/4 talonids, more distinct talonid cusps, better developed metaconids and more laterally compressed trigonids than the material described herein. Both the comparative *S. laniarius harrisii* material and Nelson Bay specimens have weaker metaconids than *S. moornaensis* and are larger than *S. moornaensis*. The new teeth are therefore assigned

Fig. 2. *Sarcophilus laniarius harrisii*, lingual view. Scale bar intervals represent 10mm.

to *S. laniarius harrisii* on the basis of close affinities to the comparative material.

Long et al. (2002), Gill (1953) and Archer *et. al.*, (1984) considered the time range of *Sarcophilus* to be early Pleistocene to present day, noting the occurrence of *S. laniarius harrisii* in many Pleistocene faunas throughout mainland Australia and Tasmania. Dawson (1982), in reviewing the taxonomic status of specimens from eastern Australian fossil localities, included *S. laniarius* fossil material no older than 30,000 years old, and considered the time range of *S. laniarius* to be Pleistocene. Guiler (1982) discussed the temporal distribution of *S. laniarius harrisii* on mainland Australia, citing fossil material no older than 5000 years old. Due to the geochronology of the bone beds in the Lower Nelson Bay Formation, the Nelson Bay material constitutes the geologically earliest recorded occurrence of verifiable age of *S. laniarius harrisii*.

The presence of *S. laniarius harrisii* in earliest Pleistocene sediments provides further information on the evolution of the sarcophilines. Archer and Bartholomai (1978, p. 5) recognized "A structural lineage starting with a hypothetical fossil form similar to *Dasyurus maculatus* Kerr, 1792, to *Glaucodon ballaratensis* Stirton, 1957, to the annectant extinct species of *Sarcophilus* and ending with *S. harrisii* is one of the best documented marsupial structural phylogenies", where the annectant species mentioned is *S. moornaensis*. *S. moornaensis* is considered early Pleistocene in age (Long et. al. 2002). The geochronology of the sediments containing the illustrated material implies *S. laniarius harrisii* may have existed contemporaneously with *S. moornaensis*, and as such *S. moornaensis* is not considered ancestral to *S. laniarius harrisii*. *Glaucodon ballaratensis* represents a sister taxon relationship to *Sarcophilus* and *Dasyurus*. Elsewhere in this issue the morphological similarities of *G. ballaratensis* to *Dasyurus maculatus* are discussed. The age of the illustrated material implies that the genus *Sarcophilus* arose at some point prior to the early Pleistocene from an ancestral form morphologically similar to *G. ballaratensis*. Future discoveries of Cenozoic and Quaternary sarcophiline material will provide further insight to the evolution of *Sarcophilus* and the placement of *Sarcophilus* in dasyurid phylogeny.

The new material in the Lower Nelson Bay Formation also provides additional information on the composition of the Nelson Bay Local Fauna and the implied environmental conditions of Nelson Bay in the early Pleistocene. Notably, the Nelson Bay Local Fauna is composed of an extensive and diverse list of macropodids of both the browsing and grazing dental grades. The presence of these forms implies a combination of palaeoenvironments may have surrounded the Nelson Bay Caldera Lake during the Pleistocene. The inclusion of arboreal forms such as the pseudocheirids suggest a forested environment may have existed close to the site of deposition, however the presence of grazing forms such as *Macropus* suggest grassland environments may have also been nearby.

Hann (1983) described the Nelson Bay Local Fauna as a biocoenosis in composition, implying the fauna once lived together prior to death and subsequent fossilisation. The Nelson Bay Local Fauna was also regarded as being derived from catastrophic mortality due to the presence of juveniles, young adults and mature adults (Hann, 1983). The

Location	Age (in years)	Reference
Strathdownie, Victoria	"Late Pliestocene"	Werderlin, 1987
Devil's Lair Cave, Western Australia	35,200 +/- 1,800	Archer, 1982
Keilor, Victoria	>18,000	Marshall, 1974
Buchan, Victoria	22,980 +/- 2,000	Flood, 1973
Lancefield, Victoria	26,000 +/- 500	Gillespie *et al*., 1978
Laura, Queensland	10,000 app.	Horton, 1977
Lake Menindee, New South Wales	18 - 26,000	Tedford, 1967
Lake Garnpung, New South Wales	>12,000	Hope, 1978
Dempsey's Lake, South Australia	>30,000	Wells, 1978
Kangaroo Island, South Australia	16,000 +/- 100	Hope et al., 1977
Queenscliff, Victoria	<10,000	Bartholomai & Marshall, 1972
Gisborne Cave, Victoria	<10,000	Gill, 1964

Table 1. Geochronologically dated fossil *S. laniarius* material from the Pleistocene and Holocene of mainland Australia

Subclass	Order	Family	Genus and species
Prototheria	Monotremata	Tachyglossidae	*Zaglossus robusta*
Metatheria	Polyprotodontia	Thylacinidae	*Thylacinus cynocephalus*
		Dasyuridae	*Sarcophilus* c.f. *laniarius harrisii*
	Diprotodonta	Thylacoleonidae	*Thylacoleo* sp.
		Ektopodontidae	*Darcius 'brailcyi'*
		Pseudocheiridae	*Pseudocheirus* c.f. *peregrinus*
			Pseudocheirus c.f. *stirtoni*
			Giant *Pseudocheirus* sp.'
		Diprotodontidae	*Diprotodon* c.f. *optatum*
			Zygomaturus trilobus
		Palorchestidae	*Palorchestes* c.f. *parvus*
		Macropodidae	*Sthenurus* sp.
			Protemnodon brehus
			Protemnodon anak
			Macropus sp.
			Macropus c.f. *titan*
			Baringa nelsonensis
			Thylogale c.f. *billardierii*
			Thylogale sp.
			Lagostrophus sp.
			Onychogalea sp.
			Setonix brachyurus
			'Very small macropodid'
		Potoroidae	indet.
Eutheria	Rodentia	Muridae	*Pseudomys* c.f. *shortridgei*

Table 2. The Nelson Bay Local Fauna, adapted from White (2002) and Herrmann (2000).

CHARACTER	*Sarcophilus harrisi* (n) = 20	*Sarcophilus moornaensis* (n) = 1	Portland *Sarcophilus* (n) = 1
M1 length	9.2	7.8	9.2
M1 width	6.2	5.2	7
M1 trigonid length	7	7.2	4.3
M1 trigonid width	4.5	5	6.4
M1 talonid width	4.9	3.2	5.9
M2 length	10.9	9.5	10.9
M2 width	6.5	5.9	8
M2 trigonid length	8.4	8.7	6.6
M2 trigonid width	5.2	3.8	5.9
M2 talonid width	3.3	4.5	4.9
M3 length	12	10	14.8
M3 width	7.4	6.3	8.7
M3 trigonid length	7.7	8	9.2
M3 trigonid width	5.6	5.4	6.6
M3 talonid width	2.3	3.3	4
M4 length	11.9	11.2	absent
M4 width	6.5	6.5	7.1
M4 trigonid length	9.9	10.2	>9.4
M4 trigonid width	4.8	4.6	>6.2
M4 talonid width	2.3	2.9	absent
P3 length	6	absent	>6
P3 width	6.7	absent	>4.4

Table 3. Comparative dental measurements of the Portland *Sarcophilus laniarius harrisii*

disconformities which truncate the bone beds in the Lower Nelson Bay Formation were correlated with periods of substantial climatic change, which may have triggered the catastrophic mortality observed by Hann (White, 2002). The disconformities represent cool, dry climates which led to the accumulation of bone material on the land surface. Subsequent flooding at the beginning of the next warm, wet phase concentrated this bone material as basal lag deposits (White, 2002). Future investigations and discoveries from the Nelson Bay Local Fauna will provide a greater insight to the nature of early Pleistocene mammalian assemblages and environmental conditions on mainland south eastern Australia.

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REFERENCES

Archer, M., 1976. The dasyurid dentition and its relationships to that of didelphids, thylacinids, borhyaenids (Marsupicarnivora) and peremelids (Peremelina: Marsupialia). *Australian Journal of Zoology, Supplementary Series*. 39: 1-34.

Archer, M., 1982. Review of the Dasyurid (Marsupialia) fossil record, integration of data bearing on phylogenetic interpretation, and suprageneric classification. In *Carnivorous Marsupials volume 2,* M. Archer ed., Royal Zoological Society of New South Wales, Sydney.

Archer, M. & Bartholomai, A., 1978. Tertiary mammals of Australia: A synoptic view. *Alcheringa* 2: 1-20.

Archer, M., Clayton, G. & Hand, 1984. A checklist of Australasian fossil mammals. In *Vertebrate Zoogeography & Evolution in Australasia (Animals in Space and Time)*. M. Archer & G. Clayton eds., Hesperian Press, Victoria Park.

Aziz-ur-Rahman, & McDougall, I., 1972. Potassium-Argon ages on the New Volcanics of Victoria. *Proceedings of the Royal Society of Victoria* 85: 61-69.

Bartholomai, A. & Marshall, L. G., 1972. The identity of the supposed dasyurid marsupial *Sarcophilus prior* De Vis 1883, with comments on other reported "Pliocene" occurrences of *Sarcophilus*. *Memoirs of the Queensland Museum* 16: 396-374.

Boitard, P., 1842. *Le Jardin des Plantes a Paris. Description et moeurs des Mammiferes de la Menagerie et du Museum d'Histoire Naturelle/ precede d'un introduction historique, descriptive et pittoresque par M. J. Janin*. J.J. Dubochet et Ce, Paris, lxvi, 472 pp.

Boutakoff, N., 1963. The Geology and Geomorphology of the Portland area. *Geological Survey of Victoria Memoir No.* 22: 52-58.

Corbett, L. K., 1985. Morphological comparisons of Australian and Thai dingoes: A reappraisal of dingo status, distribution and ancestry. *Proceedings of the Ecological Society of Australia* 13: 277-291.

Crabb, P. L., 1982. Pleistocene dasyurids (Marsupialia) from south western New South Wales. In *Carnivorous Marsupials. Volume 2.* M. Archer ed., Royal Zoological Society of New South Wales, Sydney. 511-516.

Dawson, L., 1982. Taxonomic status of fossil Devils (*Sarcophilus*, Dasyuridae, Marsupialia) from Late Quaternary Eastern Australian Localities. In *Carnivorous Marsupials. Volume 2.* M. Archer ed., Royal Zoological Society of New South Wales, Sydney. 517-525.

Environment Australia, Australian Biological Resources Study (ABRS). 2002. Australian Faunal Directory Database. *Environment Australia, Federal Department of the Environment and Heritage. 2002.* http://www.ea.gov.au/biodiversity/abrs/abif/fauna/afd/mformat.html

Flood, J., 1973. Pleistocene human occupation and extinct fauna in Clogg's Cave, Buchan, Southeastern Australia. *Nature (London)* 246(5431): 303.

Geoffroy Saint-Hilaire, E., & Cuvier, G. L. C. F. D., 1837. *Histoire naturelle des Mammiferes, avec des figures originales &c.* (Livraison 70). Blaise, Paris.

Gill, E. D., 1953. Distribution of the Tasmanian Devil, the Tasmanian Wolf and the Dingo in southeast Australia in Quaternary time. *Victorian Naturalist* 70: 86-90.

GILL, E. D., 1964. Appendix in Mahoney, J. A., 1964. The taxonomic status of *Dayurus affinis* McCoy, 1865 (Dasyuridae) and *Hysiprymnus trisulcatus* McCoy, 1865 (Macropodidae), two marsupials from a Holocene cave near Gisborne, Victoria. *Proceedings of the Royal Society of Victoria* 77: 525-533.

GILL, T. 1872. Arrangement of the Families of Mammals: with analytical tables. Prepared for the Smithsonian Institution by Theodore Gill. *Smithsonian miscellaneous collections*. 9 (1): 1-98.

GILLESPIE, R., HORTON, D. R., LADD, P., MACUMBER, P. G., RICH, T. H., THORNE, R. & WRIGHT, R. V. S. 1978. Lancefield swamp and the extinction of the Australian megafauna. *Science*. 200: 1044-1048.

GOLDFUSS, G. A. 1820. Theil 3 Handbuch der Zoologie. In *Handbuch duer Naturgesehichte: zum Gebrauch bei Vorlesungen*. G. H. von Schubert. Nurenburg.

GUILIER, E. R., 1982. Temporal and spatial distribution of the Tasmanian Devil *Sarcophilus harrisii* (Dasyuridae: Marsupialia). *Papers and Proceedings of the Royal Society of Tasmania* 116: 153-163.

HANN, L., 1983. The Vertebrate Palaeontology and Age of the Nelson Bay Formation, Portland, Victoria. *Unpublished Honours Thesis. Department of Earth Science, Monash University, Clayton, Victoria, Australia.*

HARRIS, G. P., 1808. Description of two new species of *Didelphis* from Van Diemen's Land. *Transactions of the Linnaen Society, London*. (1)9: 174-178, pl. 19.

HERRMANN, N. D., 2000. Dental analysis and palaeoecological assessment of *Baringa nelsonensis* (Marsupialia: Macropodidae: Macropodinae), and intermediate browsing/grazing kangaroo from the Early Pleistocene Nelson Bay Formation, Victoria, Australia. *Unpublished Masters Thesis. Department of Earth Science, Monash University, Clayton, Victoria, Australia.*

HOPE, J. H., 1978. Pleistocene mammal extinctions: The problem of Mungo and Menindee, New South Wales. *Alcheringa*. 2: 65-82.

HOPE, J. H., LAMPERT, R. J., EDMONSON, E., SMITH, M. J. & VAN TETS, G. F., 1977. Late Pleistocene faunal remains from the Seton Rock Shelter, Kangaroo Island, South Australia. *Journal of Biogeography* 4: 363-385.

HORTON, D. R., 1977. A 10,000 year old *Sarcophilus* from Cape York. *Search*. 10: 374-375.

ILLIGER, J. K. W., 1811. C. Illigeri ...Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis, eorumque versione Germanica. *Berolini.*

KENLEY, P. R. 1988. Southwestern Victoria. In *Geology of Victoria*, J. G. Douglas & J. A. Ferguson eds., Victorian Division, Geological Society of Australia Incorporated, Melbourne, 383-387.

KERR, R., 1792. *The Animal Kingdom, or zoological system, of the celebrated Sir Charles Linnaeus; Class I. Mammalia, containing a complete systematic description, arrangement, and nomenclature, of all the known species and varieties of the Mammalia, or animals which give suck to their young; being a translation of that part of the* Systema Naturae, *as lately published, with great improvements, by Professor Gmelin of Goettingen*. J. Murray & R. Faulder, London, 1 Pt 1 xl 400 pp. 9 pls.

LONG, J., ARCHER, M., FLANNERY, T. & HAND, S., 2002. *Prehistoric Mammals of Australia and New Guinea: One Hundred Million Years of Evolution*. University of New South Wales Press Ltd, University of New South Wales, Sydney.

MACFADDEN, M. J., MACFADDEN, P., RICH, T. H., & WHITELAW, M. J., 1987. Magnetic Polarity Stratigraphy of the Pleistocene Section at Portland (Victoria) Australia. *Quaternary Research* 28: 364-373.

MARSHALL, L. G., 1974. Late Pleistocene Mammals from the Keilor cranium site, southern Victoria, Australia. *Memoirs of the National Museum of Victoria* 35: 63-86.

MARSHALL, L. G., 1973. Fossil vertebrate faunas from the Lake Victoria region of southwestern New South Wales. *Memoirs of the National Museum of Victoria* 34: 151-171.

MERIGIAN, D., MURRAY, P. F., LATZ, P. K. & JOHNSON, K. A., 2002. The Mygoora Local Fauna: a late Quaternary vertebrate assemblage from central Australia. *The Beagle: Records from the Museums and Art Galleries of the Northern Territory* 18: 77-93.

MURRAY, P., 1991. The Pleistocene Megafauna of Australia. In *Vertebrate Palaeontology of Australasia*. P. Vickers-Rich, J. M. Monaghan, R. F. Baird, & T. H. Rich, eds. Monash Univer-

sity Publishing Committee, Melbourne, 893-1070.

OWEN, R. 1838. In *Three expeditions into the interior of eastern Australia, with descriptions of the recently explored region of Australia Felix, and of the present colony of New South Wales.* T. L. Mitchell, T & W Boone, London.

OWEN, R., 1877. *Researches on the fossil remains of the extinct mammals of Australia; with a notice on the extinct marsupials of England, Volumes 1 & 2.* J. Erxleben, London.

RICH, T. H., ARCHER, M., HAND, S. J., GODTHELP, H., MUIRHEAD, J., PLEDGE, N. S., FLANNERY, T. F., WOODBURNE, M. O., CASE, J. A., TEDFORD, R. H., TURNBULL, W. D., LUNDELIUS, E. L. *fil.*, RICH, L. S. V., WHITELAW, M. J., KEMP, A., & RICH, P. V., 1991. Appendix 1: Australian Mesozoic and Tertiary Terrestrial Mammal Localities. In *Vertebrate Palaeontology of Australasia.* P. Vickers-Rich, J. M. Monaghan, R. F. Baird, & T. H. Rich, eds. Monash University Publishing Committee, Melbourne. 1005-1070.

RIDE, W. D. L., 1964. A review of the Australian fossil marsupials. *Journal of the Proceedings of the Royal Society of Western Australia.* 47: 97-131.

SMITHSONIAN MUSEUM OF NATURAL HISTORY, DEPARTMENT OF SYSTEMATIC BIOLOGY, 1993. *Mammal Species of the World Database.* Smithsonian Institution, Washington D. C., United States of America. 1993. http://nmnhwww.si.edu/msw/

SELWYN, A. R. C. 1858. On the geology of the goldfields of Victoria. *Quarterly Journal of the Geological Society of London* 14: 533-538.

SELWYN, A. R. C., 1860. Notes on the Geology of Victoria. *Quarterly Journal of the Geological Society of London* 16: 145-150.

SRINIVISAN, M. S. & KENNET, J. P., 1981. A review of the Neogene planktonic foraminiferal biostratigraphy: Applications in the equatorial and South Pacific. *Society for Economic Palaeontologists and Mineralogists Special Publication* 32: 395-432.

STIRTON, R. A., 1957. Tertiary Marsupials from Victoria, Australia. *Memoirs of the National Museum of Victoria* 21: 121-134.

STRAHAN, R. (Ed.) 1998. The Mammals of Australia. *Reed New Holland Publishers, Sydney.*

SZALAY, F. S., 1982. A new appraisal of marsupial phylogeny and classification. In *Carnivorous Marsupials Volume 2.* M. Archer ed., Surrey Beatty & Sons Pty. Ltd. and The Royal Zoological Society of New South Wales, Mosman, New South Wales, 621-640.

THOMAS, O., 1903. Note on the technical name of the Tasmanian Devil. *Annals and Magazine of Natural History, series 7,* 11: 289.

WELLS, R. T., 1978. Fossil mammals in the reconstruction of Quaternary environments with examples from the Australian fauna. In *Biology and Quaternary environments,* D. Walker & J. C. Guppy eds. Australian Academy of Science, Canberra, 103-204.

WERDERLIN, L., 1987. Some observations on *Sarcophilus laniarius* and the evolution of *Sarcophilus. Records of the Queen Victoria Museum, Launceston* 90: 1-27.

WHITE, M. A., 2002. Formation of the vertebrate bone beds of the Nelson Bay Formation, Portland, Victoria. *Unpublished Honours Thesis, Deakin University, Victoria.*

WHITELAW, M. J., 1991. Magnetic polarity stratigraphy of Pliocene and Pleistocene fossil vertebrate localities in southeastern Australia *Geological Society of America Bulletin* 103: 1493-1503.

WROE, S., EBACH, M., AHYONG, S., DE MUIZON, C., & MUIRHEAD, J., 2000. Cladistic analysis of Dasyuromorphian (Marsupialia) phylogeny using cranial and dental characters. *Journal of Mammalogy* 81(4): 1008-1024.

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